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### A SKETCH OF THE HISTORY OF FERN CLASSIFICATION

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During the two centuries since the beginnings of formal classification the group of ferns has grown from less than 200 to approximately 10,000 species. Against this background of ever-increasing knowledge, augmented later by the theory of evolution, the classification of ferns has developed. With the considerable present-day interest in the ferns from the viewpoints of paleobotany, anatomy, cytology and morphogenesis, as well as systematics itself, it is certainly desirable to understand our present classification, its basis and its problems. While these might be stated categorically, they can only be understood in the light of their history. Although J. E. Smith (1810), John Smith (1875) and Jean-Édouard Bommer (1867) have, among others, published good reviews of the earlier fern classifications, it will be desirable to follow these again as well as the more recent developments. One cannot, in a brief review, mention all of the authors who have contributed materially to our present classification of ferns nor is it even possible to do justice to the few selected. Rather, I will trace the more important trends in classification and mention some of the most significant authors and their works by way of illustration.

On the authority of Sir J. E. Smith we may pass by the seventeenth and early eighteenth century authors, for as he has said (Smith, 1793, p. 401<sup>1</sup>): "The Genera of Ferns, entirely neglected by the older botanists, and but slightly or superficially touched upon by systematic writers of the last century, were first attempted to be reduced to fixed principles by Linnaeus." The shape of the sorus and its position on the leaf afforded Linnaeus (1753, 1754) the primary characters for his genera. He recognized 11 genera of Filicales<sup>2</sup> in his *Cryptogamia Filices* and about 175 species. This was a highly artificial arrangement, species of quite distant relation

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<sup>1</sup>In this and the next quotation the reference is to the original paper, but the quotation is from the English translation (1798).

<sup>2</sup>The works to be discussed differ considerably in their scope—some are complete, some omit one family, others omit several families. As a matter of convenience, the number of genera given for each classification is that of the Filicales as presently defined, i.e., the Leptosporangiatæ. All authors include the largest family, the Polypodiaceæ, *sens. lat.*, and the inclusion or omission of the smaller families does not greatly alter the comparative value of the numbers.



being placed together, yet it was a beginning and served a utilitarian purpose in placing newly described species until it was succeeded by a more natural system. It was not that Linnaeus' characters were at fault, for we still use them today, but rather that they alone are quite inadequate to establish natural genera.

Characters of the indusium were first used effectively by Sir James Edward Smith (1793) some 40 years after Linnaeus. Smith recognized 20 genera based on characters of the shape of the sorus, its position on the frond, the shape and placement of the indusium and the manner of its opening. He expressed his views on the importance of the indusium, particularly the manner of its opening, in these words (Smith, 1793, p. 405): "This circumstance no one has yet considered; yet it is undoubtedly of the greatest use in determining natural genera, being not only constant in every species, but in ferns whose habit and other particulars agree, it is always found to be similar." Smith's classification is also the first to be presented as a natural system. Since his time authors have basically agreed on the need for a natural system but beyond this there has been, as we shall see, much diversity of opinion. It would probably be difficult to improve on Smith's system so far as the species he knew are concerned. However, in retrospect we can see that he underestimated the group he was classifying by using only characters of the fruiting parts to define his genera.

The first handbook of ferns, by Olof Swartz (1806), treated 33 genera and something less than 700 species. Swartz used the same characters of the sorus and indusium as established by J. E. Smith, and his book represents the first fully elaborated treatment of Smith's system. In spite of the fact that many of Swartz's genera were large and unnatural, they were accepted until three decades later. In the interim new genera were described, but on the same basis as before. One of the most elaborate classifications following the Swartzian system was published by Niçaise Augustin Desvaux (1827). He recognized 66 genera of Filicales, an increased number due to a more detailed analysis of characters of the indusium and of the disposition of the sporangia.

Actually, the naturalness of Smith's system was in part passé even before Swartz's elaboration, and it certainly was entirely so by the time of Desvaux's classification. However, the recognition of additional genera based on increased study of the sorus and indusium did make the latter system more natural than Swartz's. It is now fully apparent that new species were being added so rapidly that most genera could not be maintained as reasonably natural groups without splitting them on the basis of new characters. Perhaps one reason that this was so long delayed was that the known ferns could all be conveniently placed into genera based solely on the characters of the sorus and indusium. However usable, this system was finally challenged since too many species, diverse in other characters, were all mechanically placed in one genus.

The notable revision of fern genera by Karel (Carolo) Boriwog Presl (1836) introduced new, essentially modern, principles of classification. He used vegetative characters as well as those of the fructification, placing special emphasis



upon the venation. In addition he used characters of habit, of the rhizome, position of the leaves, number of vascular bundles in the petiole, and the nature of the indument. He discussed and illustrated spore characters, although he did not make use of them in his classification. Presl recognized 117 genera in 1836 and added 59 more in his later publications (1843, 1845, 1852). That generic characters may be drawn from any part of the plant—their value being dependent upon their behavior and correlation with other characters—and that the vegetative organs may furnish characters of equal or even more importance than the fruiting organs became evident in the work of Presl. Although his system has been corrected in many ways his methods are still valid.

Presl must be given credit as the founder of modern pteridology in point of time, but actually this should be shared almost equally with John Smith who worked out a revision of genera independently. Smith (1841-1843), although differing on generic limits, employed essentially the same kind of characters as Presl, generally placing strong emphasis upon venation and vegetative characters. He recognized 138 genera of Filicales. The independent publication of two such similar classifications simultaneously would seem to emphasize that the time was ripe for the introduction of new principles.

The new approach to classification was hardly well founded, however, before it was effectively challenged from an authoritative position. Sir William Jackson Hooker, Director of the Royal Botanic Gardens, Kew, had provisionally accepted many of John Smith's and Presl's genera in his 'Genera Filicum' (Hooker & Bauer, 1838-1842). A few years later (Hooker, 1844-1864), he began publication of his monumental 'Species Filicum'; he comments in the introduction (Hooker, 1:xiv):

Increased study has, he must confess, strengthened his conviction that those Botanists, who have showed themselves peculiarly addicted to multiplying genera, have not always taken Nature for their guide, nor succeeded in eliciting a simple and tangible arrangement. . . . In these remarks Dr. Presl and Mr. John Smith are particularly alluded to.

Hooker recognized only 63 genera and based them on the classical characters of sorus and indusium. He did not deny the naturalness of many of Presl's and John Smith's genera and treated them as subgenera or sections. In his free use of these subgeneric categories—89 of them—Hooker probably strove for a middle course between the large unnatural established genera and the smaller, relatively natural ones of Presl and John Smith. As we see it now, this was not a particularly successful attempt since in the large genera the section became of equal importance to the genus itself.

There seem to be two basic differences in the viewpoints of Hooker and those of Presl and Smith. Hooker required that genera be based on characters of the fruiting parts (vegetative characters were of subgeneric or sectional value), and he emphasized utility; Presl and Smith, using all characters, recognized a major natural group of species as a genus and emphasized naturalness. Perhaps in his day Hooker's was philosophically the sounder view, supported strongly by ex-



perience in the classification of the flowering plants. Or perhaps Presl and John Smith had an insight into the ferns that enabled them to see the limitations imposed in this particular group by the fruiting structures. In all events, for the next half-century Hooker's system dominated pteridology and prolonged the life of the Swartzian system to nearly a full 100 years. It was not effectively opposed until nearly the 20th century.

Probably the most elaborate 'Genera Filicum' was written by Antoine Laurent Apollinaire Fée (1850-52). Fée followed the Preslian school but used an even greater variety of characters. He recognized 181 genera with an additional seven of doubtful status. The fine lithographs of J. A. Villemain present details of the venation, sorus, indusium, indument, sporangium and spores. In addition to vegetative characters, Fée sought to find new characters in the fruiting structures and introduced the number of the cells of the annulus of the sporangium. Fée compared the value of this character in the ferns to that of the peristome in the classification of the mosses although subsequent study has hardly confirmed his optimism. In spite of his detailed study of this character it was not used again in a major classification until Copeland's recent 'Genera Filicum.'

Having finished his 'Species Filicum' in 1864, Hooker commenced a synoptical handbook of the species of ferns in order to place the more important information of his previous publication before the public in a more convenient form. His 'Synopsis Filicum' was completed after his death by John Gilbert Baker (Hooker & Baker, 1865-1868). The treatment of genera is almost identical to that of the 'Species Filicum' and it remained the same in the second edition of 1874. The importance of the 'Synopsis Filicum' is that it was the first handbook of ferns since that of Swartz in 1806, and its great utility was a very important factor in carrying to general acceptance the Hookerian System. Such a synopsis of species was never published by the followers of Presl.

Although John Smith was preceded by Presl in laying the foundations of the modern system, he fully established his own position by his later publication, the 'Historia Filicum' (Smith, 1875). This publication not only presented his own matured views but also integrated the numerous genera of Presl and Fée. He recognized 212 genera of Filicales, three times as many as the 'Synopsis Filicum' of 1874. Smith was the founder and curator of the living fern collection at Kew and under his care it became one of the most notable ever assembled. He had an intimate knowledge of his plants, and this is reflected strongly in his classification. Smith's views, however well founded upon observation of the living plant, were nevertheless largely ignored until the twentieth century.

The first breach in the dominance of the Hookerian system was made by Hermann Christ (1897), and it was effectively widened by Ludwig Diels in his treatment in the 'Natürlichen Pflanzenfamilien' (1898-1900). Although Christ recognized only 92 genera he did emphasize vegetative characters for genera and this basis was enlarged upon by Diels. The latter author recognized 130 genera (including Sadebeck's treatment of Hymenophyllaceae). Diels thus had almost twice as many genera as the 'Synopsis Filicum'. He gave new impetus to classifica-



tion, particularly phyletic classification which was in its initial stages. Diels attempted a phyletic presentation based on characters of the sorus and indusium. Such a basis has not actually been discredited, but in general it has been slighted by the present emphasis upon vegetative characters.

The work of Diels also stands as a landmark for the modern usage of the family as a formal category. Previous authors rarely used the family category; the major groups of genera or tribes were usually called orders or suborders. Robert Brown (1810) recognized some of the essential differences of the sporangia that were to form the primary characters for the fern families. Carl Frederick Phillip de Martius (1828–1834) listed seven major groups of his Filices, and they generally correspond closely to our modern families in form of name, characters and content but he did not designate their category. A year later (Martius, 1835) he changed this classification somewhat, recognizing five orders of ferns and under the order Filices he had seven families. These groups are without description and by comparison with the classification of the angiosperms it is clear that his category order corresponded to our modern family. Georg Mettenius (1856) brought previous usage even closer to our own, with the exception that again he used the category order for the equivalent of our family. The sporangial characters and content of his orders are very similar to those of the families of Diels. As an indication of the instability in the use of the higher categories it may be noted that while Martius had families as subdivisions of his orders, Mettenius reversed this and divided the family Filices into eight orders. Christ (1897) had major groups very similar to those of Diels but did not designate their rank. Thus although the characters of the annulus and capsule had rather early been established, our families in their modern sense and usage begin with Diels.

There was a period of great activity during the next two decades in which new genera were described and old ones revived, and, perhaps of more importance, a basis of fact was laid for a real phyletic system of classification. The studies of Karl Eberhard Ritter von Goebel, summarized in his 'Organographie' (1898–1901, 1918) and of F. O. Bower (1894–1904, 1910–1923) on the growth, development, anatomy and morphology of the fern plant, and particularly those of Sir Albert Charles Seward (1900, 1910) and Dukinfield Henry Scott (1908) on fossil ferns made a phyletic classification possible. At least, with such a broad basis of comparison, certain relations could be fairly well deduced, although others remained as largely speculative.

The first really phyletic classification was by Frederick Orpen Bower (1923–1928) who developed his phylogeny on a broad basis of anatomical, morphological, and developmental characters. He recognized twelve families of Filicales and six lines of evolution in the Polypodiaceae. Primarily due to the consideration of the difference between the marginal and superficial sorus as fundamental, these lines within the Polypodiaceae were treated as three quite independent developments. This proposal of polyphyletic for the traditional fern family is the most striking and most debated aspect of his treatment. Bower's elaborate three-volume work



is the best documented account of fern phylogeny. However, his interests were not in formal taxonomy and although he recognized separate groups of the Polypodiaceae he did not propose a system to accommodate them.

Edwin Bingham Copeland (1929) was the first systematist to deal with the problem of recognizing the polyphyletic origin of the Polypodiaceae in a formal classification. He points out that there are two alternatives, (1), to raise each phyletic line to the rank of family, or (2), define the Polypodiaceae so as to include the older types and make it monophyletic. He considers neither as free of objection but adopted the latter course. His Polypodiaceae includes the Plagiogyriaceae, Cyatheaceae, Dicksoniaceae, Matoniaceae and Dipteridaceae of Bower. Such a group, according to Bower's views, however, would not be monophyletic. A unique feature of Copeland's treatment is his interesting system of numbering the genera in such a manner as to show their place in the phyletic tree or bush. This or a similar system might be considered as a possible means of circumventing the difficulty of expressing phylogeny in a necessarily linear presentation of the genera in book form.

Carl Christensen (1938) published the first complete taxonomic synopsis that took into account the modern advances. He recognized twelve families of Filicales and about 230 genera which were based on a wide variety of characters. He divided the Polypodiaceae into fifteen subfamilies although he states in the text that perhaps it would be better to treat them as families. Within each family or subfamily the genera are arranged in a generally phyletic sequence. In considering the subfamilies Christensen agrees with Copeland, and disagrees with Bower in stating (*loc. cit.*, p. 534): "They are not very closely related to each other but probably separate branches from an ancient common stock. . . ." As a matter of opinion and of convenience he does not include the closely related families within the Polypodiaceae, as Copeland did, but rather defines the family on the basis of the sporangium.

Three recent studies have added new views on the phyletic classification of the fern families. Ren-Chang Ching (1940) divided the Polypodiaceae into 32 families which were grouped into seven distinct lines of evolution. In general, these are the same lines that Copeland later recognized as families. Ching's work is poorly, if at all, documented in so far as justification of his recognition of the numerous families is concerned. It can hardly be given serious consideration unless we are quite ready to reject the present usage of the family category. Frederick Garrett Dickason (1946) inclines to question the full validity of many of Bower's tenets, and in particular he points out possible weaknesses in the derivation of the polypodiaceous sporangium from several different sources and the derivation of the marginal and superficial Polypodiaceae from similar marginal and superficial Simplices. Dickason accepts the numerous families of Ching but implies that the main groups of families arose more or less simultaneously from a common basic plexus. Richard Eric Holttum (1947) also attacks the validity of certain of Bower's expressed relationships and presents a revised classification of



the Polypodiaceae. He recognizes five families, the largest, Dennstaedtiaceae, containing eleven subfamilies. This family, although natural, he admits as undefinable. Especially notable in Holttum's work is the use of characters of the type of cutting and branching pattern of the leaf and also of his essentially complete denial of the basic difference of the superficial and the marginal sorus, genera of both kinds being placed in the same family.

The latest phyletic classification is by Copeland (1947) who now essentially accepts the polyphyletic classification of the Polypodiaceae as envisioned by Bower. He recognizes three major independent lines and classifies these in eight families. Eleven additional families of Filicales bring the total to nineteen. He has 299 genera based on a wide variety of characters and these correspond in principle, as do those of Christensen, to the genera of Presl, Fée and John Smith. In adopting separate families for the lines of evolution of the Polypodiaceae Copeland has lost definition of his groups. In fact, he freely admits Pteridaceae and Aspidiaceae as natural but undefinable. This is a consequence of his philosophical principle that a family or genus must be natural and only secondarily should be convenient. This treatment brings to the fore, perhaps more forcibly than ever before, the conflict between naturalness and utility in classification.

The next major system will necessarily be most concerned with two issues. One is the phylogeny of the Polypodiaceae, *sens. lat.*, involving primarily the nature and origin of the sporangium and the phyletic relation between marginal and superficial sori. The other is the conflict between utility and naturalness mentioned above. The first issue must still be worked out since it cannot be now considered that the phylogeny of the Polypodiaceae is sufficiently known. As to the second issue, it is now evident, at least in the ferns, that a single classification cannot have a maximum of both utility and naturalness. Bower has expressed what is probably an accurate estimate of the relation of the two types of classification (Bower, 1928, vol. 3, p. 39):

"A complete artificial classification is always possible and is indeed necessary for floristic use. A complete phyletic classification will only become possible with complete knowledge of the descent of the organisms classified. The second cannot replace the first under present conditions, owing to the imperfection of present knowledge. But it can lead to a correction and amendment of classification for floristic use, so as to make it run ever more nearly along lines of probable evolution."

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